

EVOLUTION OF SEXUAL SYSTEMS IN FLOWERING PLANTS¹

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ABSTRACT

The diversity of sexual systems in plants has been generally attributed to selection for an optimal amount of genetic recombination. However, sexual systems such as hermaphroditism (including heterostyly), monoecism, andromonoecism, gynomonoecism, dioecism, androdioecism, and gynodioecism may also be viewed as different patterns of relative resource allocation to paternal and maternal functions to optimize paternal and maternal reproductive success in different ways. These different patterns may arise in large part in response to reproductive competition resulting from sexual selection. But the efficacy of sexual selection in zoophilous species is mainly determined by pollinator behavior. It follows then that the evolution of a particular sexual system must be influenced by the dynamics of the pollination system. The role of pollinators in the evolution of sexual systems is examined by considering several types of interactions between flowers and pollinators. The role of cost-sharing between paternal and maternal functions in pollinator attraction is stressed in the evolution of hermaphroditism. Andromonoecism is considered in terms of loss of pistils in that part of the flower crop which is produced merely to attract pollinators and/or to fulfill male function. In the evolution of andromonoecism to monoecism, the role of stamens of hermaphroditic flowers in the functional integrity of the pollination system is evaluated. The importance of long mouth parts of pollinators to promote compatible pollinations in the evolution of heterostyly is pointed out. The evolution of protogyny is considered in relation to long inhabitation of pollinators in flowers and inflorescences. The evolution of dioecism is examined in relation to the ability of pollinators to respond to minor changes in floral resources thereby altering the patterns of pollen donation and pollen receipt. Finally, the importance of stamens in hermaphroditic plants in attracting pollen collecting bees is emphasized in the maintenance of androdioecism. The development of a general hypothesis to explain the diversity of sexual systems will require not only a comprehensive knowledge of pollination ecology but also a revision of the sexual system classification that will take into account functional gender rather than intrinsic gender estimates based solely on morphology.

The flowering plants display a wide variety of sexual systems ranging from obligate selfing in association with self-compatibility to obligate outcrossing in conjunction with self-incompatibility (Darlington, 1958; Grant, 1958; Lewis & John, 1963; Mather, 1973; Solbrig, 1976; Jain, 1976; de Nettancourt, 1977). In addition, genetic recombination may be partially or completely circumvented by facultative or obligate apomixis (Stebbins, 1950). Superimposed upon these genetic systems are such temporal and morphological mechanisms as protandry, protogyny, heterostyly, monoecism, andromonoecism, gynomonoecism, dioecism, gynodioecism, and androdioecism, that are also presumed to regulate the level of outcrossing (see Darwin, 1877; Müller, 1883; Mather, 1940; Lewis, 1942; Baker, 1959; Jain, 1961; Lloyd, 1975a; Ross, 1970; Charlesworth & Charlesworth, 1978; Charlesworth & Charlesworth, 1979; Ganders, 1979).

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Darwin (1877) was the first to comprehensively document and explain the diversity of sexual systems in plants. His work, including his studies of the effects of self- and cross-fertilization on the fitness of plants (Darwin, 1876), had a major impact on current ideas about the evolution of sexual systems. After the development of the synthetic theory of evolution, the genetic implications of the diversity in sexual systems emerged as a major issue in the evolutionary biology of plants, and selective pressure for an optimal amount of recombination came to be viewed as *the essential force* in the evolution of sexual systems (Stebbins, 1958; Darlington, 1958; Grant, 1958; Baker, 1959; Lewis & John, 1963; Mather, 1973). In turn, patterns of plant sexuality came to be regarded as outcrossing mechanisms and regulators of genetic recombination.

Recently, models have been proposed for the evolution of some sexual systems that do not invoke outcrossing as the main selective force. Charnov et al. (1979) and Maynard Smith (1978) have postulated the evolution of hermaphroditism, dioecism, and gynodioecism in terms of optimal allocation of resources to male and female reproduction. Janzen (1977) has commented upon the effect of optimal mate selection on the evolution of monoecism and dioecism. The evolution of dioecism has also been examined in the context of sexual selection (Willson, 1979; Charnov, 1979; Bawa, 1980a; Givnish, 1980), dispersal by avian frugivores (Bawa, 1980a; Givnish, 1980; see also Lloyd, 1981), foraging behavior of pollinators (Beach & Bawa, 1980; Beach, 1981), and disruptive selection resulting from differential utilization of habitats by male and female plants (Freeman et al., 1980). Pleiotropic effects of male sterility gene have been implicated in the evolution of gynodioecism in *Plantago lanceolata* (Krohne et al., 1980).

There are two major difficulties with the general explanation that selective pressure for outcrossing or an optimal amount of recombination underlies the diversity of sexual systems. First, the argument might explain the evolution of self- versus cross-fertilization but does not account for the tremendous diversity of sexual systems, almost all of which facilitate outcrossing (Willson, 1979). It is possible that different sexual systems result in different levels of outcrossing, but there is no evidence that as one moves from andromonoecism and gynomonoeism to dioecism, one moves along a consistent gradient of increasing cross-pollination. In fact, several andromonoecious, monoecious, and gynodioecious species are known to be self-incompatible (see below). Second, it has been demonstrated that the ability to self- or cross-fertilize, by itself, is often not a good indicator of the level of recombination in natural populations (see Allard, 1965; Jain, 1976), because the level of recombination is determined not only by the sexual system but also by the mechanics of crossing-over, linkage (Darlington, 1958; Lewis & John, 1963), the foraging behavior of pollinators and seed dispersal agents (Levin & Kerster, 1974), and selection against inbreeding (Jain, 1976).

Our discussion of the evolution of flowering plant sexual systems is developed with repeated emphasis of some basic ecological differences between paternal and maternal reproductive success (Horovitz & Harding, 1972; Charnov, 1979; Lloyd, 1979a, 1980b; Willson, 1979). Our approach is based on two proposals. The first is that paternal reproductive success is limited by a plant's ability to disperse pollen to conspecific stigmas, whereas maternal success is usually limited by the amount of nutritional resources available for developing embryos, seeds,

and fruits (Bateman, 1948; Charnov, 1979; Lloyd, 1979a). Thus, paternal and maternal reproductive success may be optimized in different ways. The second proposal is that conspecific pollen movement, in particular patterns of dispersal and receipt, is greatly constrained by the type of pollinator or pollination system. We suggest that: (a) sexual systems such as hermaphroditism (including heterostyly), monoecism, andromonoecism, gynomonoecism, dioecism, androdioecism, and gynodioecism be viewed as different patterns of relative resource allocation to paternal and maternal functions to optimize paternal and maternal reproductive success in dissimilar ways (see also Charnov et al., 1976; Lloyd, 1979a); (b) that these different patterns arise mainly in response to reproductive competition resulting from sexual selection (Willson, 1979); and (c) that the evolution of a particular pattern is constrained largely by the dynamics of the pollination system. The last point, being new and a crucial element in our proposal, needs elaboration.

Although sexual selection influences the relative *allocation* of resources to male and female functions (Charnov, 1979; Willson, 1979), the actual *distribution* of these resources in the form of male, female, and bisexual flowers is largely determined by the ecology of the pollination system. In the case of biotic pollination, this is a result of the foraging behavior of pollinators determining the pattern of pollen removal and pollen receipt, and consequently the effective role of flowers as pollen donors and pollen receivers (Willson & Price, 1977; Pyke, 1978). But the foraging behavior of pollinators itself is influenced by selection in plants for variation in floral rewards in space and time to optimize the movement of pollinators and thereby pollen flow. Variation in floral rewards may be achieved through changes in the relative proportions of male, female, and bisexual flowers, or of pollen donors and pollen receivers, because male flowers may only produce pollen or pollen as well as nectar, whereas female flowers generally secrete only nectar except in cases involving mimicry (Baker, 1976; Bawa, 1980b). Many sexual systems may simply represent such variations that have coevolved with the foraging behavior of pollinators. Our treatment of sexual systems here emphasizes such coevolution and the role of pollinators in differentially influencing paternal and maternal reproductive success.

In addition to the putative ecological and energetic advantages of different patterns of floral sexuality that we review below, a number of attempts have been made to elucidate the adaptiveness of hermaphroditic organisms (in the broad sense, to include, for example, monoecious plants) over unisexual individuals (Baker, 1967; Maynard Smith, 1978; Heath, 1977; Charnov, 1979; and see Lloyd, 1981, for several additional references). Although these proposals are relevant to the adaptive nature of hermaphroditism vs. unisexuality at the individual level, we limit our discussion here to the ecology of floral sexuality.

We have avoided the use of the term *breeding system* throughout the paper in favor of *sexual system*. This seems more appropriate as it does not carry the implication that plant gender is the sole result of selection for a certain level of genetic variability. The sexual system does include those factors that directly influence the level of outcrossing, but we view the distribution of male and female functions in space and in time, and the ecological interactions among individuals that mate with each other, as being primarily the result of the coevolution between sexual partners and also between flowers and pollinators.

TABLE 1. Standard classification of flowering plant sexual systems as currently used.^{a,b}

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- A. Systems based on the spatial distribution of male and female reproductive organs.
- I. Sexually monomorphic^c systems characterized by only one gender class of individuals.
 1. *Hermaphroditism*: Plants bear only bisexual flowers.
 2. *Monoecism*: Plants bear male and female flowers.
 3. *Andromonoecism*: Plants bear bisexual and male flowers.
 4. *Gynomoecism*: Plants bear bisexual and female flowers.
 - II. Sexually dimorphic species characterized by two gender classes of individuals.^d
 1. *Dioecism*: Plants bear either male or female flowers.
 2. *Gynodioecism*: Plants bear either female or bisexual flowers.
 3. *Androdioecism*: Plants bear either male or bisexual flowers.
- B. Systems based on the temporal distribution of male and female organs.
1. *Protandry*: Pollen removed from the anthers before stigmas attain receptivity.
 2. *Protogyny*: Stigmas become receptive before anthers release pollen.
- C. Systems based on the presence or absence of self-incompatibility alleles.
1. *Self-incompatibility*: Plants polymorphic with respect to the presence of self-incompatibility alleles; pollinations involving pollen and stigma sharing the same self-incompatibility alleles, including self pollinations, result in no fruit set.
 2. *Self-compatibility*: Plants monomorphic and without the presence of self-incompatibility alleles; all pollinations, including self-pollinations, result in fruit set.
- D. Systems based on variation in style and stamen length.
1. *Distyly*: Two types of individuals that bear different forms of flowers, pin flowers with long styles and short stamens and thrum flowers with short styles and long stamens. Self-pollination and pollination within the morphs generally incompatible.
 2. *Tristyly*: Three types of individuals that bear long-, mid-, or short-style flowers. Anthers occupy two out of the possible three positions, for example, long-style flowers have anthers at the short and mid position, mid-style flowers have anthers at the short and long position, and so on. Compatible pollinations result from crosses involving stigmas and anthers at the same level.
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^a In addition to the systems described below, there exist other systems such as cleistogamy and various forms of apomixis (see Stebbins, 1950).

^b The systems described below are not mutually exclusive.

^c The use of monomorphic and dimorphic follows that of Lloyd (1972a, 1979a, 1980a). These terms should not be confused with their application elsewhere, usually to describe floral heteromorphism based on variation in style and stamen length (Ganders, 1979).

^d Plants of sexually dimorphic species may exhibit considerable variation in sex expression, especially in gynodioecious species in which individuals with bisexual flowers may be partially or fully female-sterile.

CLASSIFICATION OF SEXUAL SYSTEMS

Lloyd (1980a) has pointed out difficulties with the existing classification of flowering plant sexual systems. The descriptive terms used by taxonomists and ecologists alike, being derived from Linnaeus's (1737) artificial classification of flowering plants based on sexual systems, are typological, qualitative, and defined by arbitrary limits. Because of this and for additional reasons (see Discussion) the available terminology neither adequately describes patterns of sexuality in plants, nor their effective gender. The work of Lloyd (1980a) in establishing quantitative measures of plant gender is of great value. However, for purposes of our initial discussion, we will use the traditional sexual system categories as shown in Table 1.

SEXUALLY MONOMORPHIC SYSTEMS

Hermaphroditism.—We use the term *hermaphrodite* in a restricted sense to designate those species with simultaneously bisexual flowers.

Most flowering plants have only bisexual flowers (Yampolsky & Yampolsky, 1922; Lloyd, 1981) and have their pollen distributed by a diverse array of biotic

and abiotic agents (Faegri & van der Pijl, 1971). The ecological and evolutionary significance of bisexuality was emphasized by Baker & Hurd (1968), who suggested that the coevolution of hermaphroditic flowers with animal pollination might be an important advancement by early angiosperms since pollen-producing and pollen-receiving organs in the same flower allowed for efficient simultaneous deposition and removal of pollen. Baker & Hurd (1968) and Crepet (1979) have argued that since the original attraction of visiting insects for flowers was the presence of pollen for food, there would have been no incentive for pollinators to visit a female flower, giving an advantage to plants with hermaphroditic flowers.

Charnov et al. (1976) and Maynard Smith (1978) have proposed that bisexual flowers sometimes represent the optimal use of energetic resources available for reproduction, since the fixed costs associated with male and female functions would be shared. Such costs would include, for example, bracts subtending flowers, pedicels supporting flowers, flower parts that serve in pollinator attraction, and nectar rewards.

It is significant that in contrast to sexually dimorphic species, hermaphroditic species generally have large, showy flowers (Bawa & Opler, 1975; Bawa, 1980a). Dioecism is poorly represented in the Araceae and Palmae in which the energetic investment into large bracts (spathes) and inflorescence stalks (spadices) presumably far exceeds the investment into very small male and female flowers. These correlations are consistent with the hypothesis that whenever common costs of male and female functions are large relative to the costs of the production of the two types of gametes, hermaphroditism may be favored over unisexuality (Heath, 1977; see also Lloyd, 1979a). Note, however, that Heath (1977) proposed the hypothesis to explain the evolution of hermaphroditism vs. unisexuality in animals and that he defined hermaphroditism in a broad sense to cover monoecious as well as hermaphroditic species.

It is difficult to assign a single most important selective force to the evolutionary rise and maintenance of bisexual flowers because, ecologically, hermaphroditism encompasses a diverse group of plants. The production of functional male and female gametes does not mean that either the flower or the individual plant contributes to the next generation equally via the male and female pathways (Horovitz & Harding, 1972; Lloyd, 1979a; Willson, 1979). Willson & Rathcke (1974) and Willson & Price (1977) have provided evidence that in milkweeds (*Asclepias* spp.) an increase in the number of flowers in an inflorescence results in a greater genetic contribution via pollen to the next generation, but not via ovules. In addition, phenomena such as dichogamy, self-incompatibility, and heterostyly make hermaphroditic species a complex assemblage of plants.

Andromonoecism.—Andromonoecism has been reported in species pollinated by bats (Heithaus et al., 1974), bees (Bell & Lindsey, 1978; Symon, 1979; Bertin, 1981), bees and flies (Primack & Lloyd, 1980), hummingbirds (Bertin, 1981), and moths (Bawa, unpublished data). In grasses, andromonoecious species are wind pollinated (Connor, 1979).

The evolution of andromonoecism has been generally ascribed to selective pressure for increasing cross-fertilization (e.g., Heithaus et al., 1974), but this explanation is incomplete for several reasons (Primack & Lloyd, 1980), including the existence of self-incompatibility in several andromonoecious species (Zapata

& Arroyo, 1978; Bawa, unpublished data), and thus other selective forces for the evolution of the sexual system should be considered.

It is a common observation that many hermaphroditic plants generally bear many more flowers than the number of fruits that are matured (see Bawa, 1974, for fruit/flower ratios in several species). Those flowers that do not set seed may function to either attract pollinators and/or to disperse pollen (Willson & Price, 1977; Lloyd, 1979a). Andromonoecism can simply be regarded as representing the situation in which nonfunctional pistils are aborted prior to flowering in those flowers that are destined to serve male or attraction functions (Zapata & Arroyo, 1978). However, it is noteworthy that andromonoecism, though widely distributed, is relatively rare as compared to hermaphroditism, whereas the phenomenon of "excess" flower production is very common in flowering plants. The question then arises as to the significance of pistils in hermaphroditic flowers that largely act as pollen donors. Three possibilities might be considered. First, in many species, especially those with extremely specialized pollination mechanisms, e.g., Apocynaceae and Orchidaceae, the abortion of pistils could disrupt the pollination system by structurally perturbing the floral morphology. Second, the abortion of pistils in many flowers before pollination could restrict the efficacy of selection on progeny acting through control over pollen germination, pollen tube growth, and embryo and fruit abortion. Third, pistils may not be aborted in most species because there is no predictability before pollination with respect to the fate of flowers as pollen donors and pollen recipients (Lloyd, 1980b).

Additional factors in the evolution of andromonoecism have been recently explored by Primack & Lloyd (1980).

Gynomonoecism.—As compared to andromonoecism, gynomonoecism is restricted in its distribution, being known in less than half a dozen families (Yampolsky & Yampolsky, 1922). The Compositae contains the greatest number of gynomonoecious taxa (Lloyd, 1979a). Unfortunately, unlike andromonoecism, detailed information about the pollination biology of gynomonoecious species is not available. In the Compositae gynomonoecism results from the sterilization of stamens in the ray (peripheral) florets of the inflorescence. By being petaloid the ray florets enhance the attractiveness of the inflorescence consisting of small flowers. This gives the inflorescence a flowerlike structure, and makes it a functional pollination unit. It is possible that in this family the selective pressure for attractive petaloid ray florets has led to the sterilization of stamens; the large size of male-sterile florets in the Compositae, and of male- and female-sterile flowers in *Viburnum* and other genera raises the possibility that the resources expended in stamens and pistils may be easily reallocated to other floral organs such as petals. Indeed, by attracting pollinators, ray florets in the Compositae influence the level of outcrossing. However, a consideration of gynomonoecism as a pollination rather than an outbreeding system makes it easier to explain why the vast majority of gynomonoecious species occur in the Compositae.

Lloyd (1979a) suggests two other factors to account for the evolution of gynomonoecism in the Compositae. One is that the increase in the number of "polliniferous" flowers in the capitulum would result in neither greater floral display nor an increase in the number of visits by pollinators since it is the capitulum rather than the individual flowers that functions as the unit of attraction. The

other is that in a capitulum composed of uniovulate flowers, gynomonocism may be the only way to increase the number of seeds without increasing the number of "polliniferous" flowers.

Monoecism.—The sexual specialization of flowers represented by andromonoecism and gynomonocism is carried a step further in monoecious taxa that are characterized by the presence of male and female flowers on the same plant. Contrary to the popular viewpoint (Yampolsky & Yampolsky, 1922; Grant, 1951; Stebbins, 1951; Faegri & van der Pijl, 1971; Charlesworth & Charlesworth, 1979) monoecism is not confined to wind-pollinated plants. In tropical forests a large number of zoophilous species are monoecious. The vast majority of monoecious species in a dry deciduous and a wet evergreen forest in the lowlands of Costa Rica are insect pollinated, a few are hummingbird pollinated (Bawa, unpublished observations).

It has been argued that monoecism has evolved as a result of the selective advantages of cross-fertilization (e.g., Maynard Smith, 1978), though Godley (1955) has demonstrated the presence of self-incompatibility in several species. We propose that evolution of monoecism represents the continuation of the trend seen in andromonoecious species towards the specialization of flowers into pollen donors and pollen recipients which is due in part to sexual selection and in part to the mechanics of pollination. Monoecism can arise in one step from andromonoecism by the sterilization or abortion of the stamens in hermaphroditic flowers. In relation to the role of pollinators in the evolution of monoecism, we discuss the conditions under which andromonoecism might evolve into monoecism and the conditions under which andromonoecism remains stable.

Selection for the sterilization or abortion of stamens in hermaphroditic flowers may occur under two conditions. The first condition is when pollen in the flowers interferes with the deposition of incoming cross-pollen (Bawa, 1980a). Such interference is likely when the pollination mechanism is imprecise and flowers are small and closely aggregated in an inflorescence, e.g., Araceae, Euphorbiaceae, Moraceae, Palmae, and others. In many taxa of these families, not only is there spatial separation, but also temporal separation of male and female flowers, suggesting perhaps the role of interference as well as sexual selection in the spatial and temporal differentiation of male and female functions. Interference is also likely when pollen is picked up from and deposited on the inflorescence during the same foraging trip, as is the case in some protogynous, monoecious aroids. In other words, if the male and female phases cannot be separated in time in the same flower, they might be separated in space, and by further evolution in space and time. It is noteworthy that many andromonoecious species have large flowers, when contrasted with monoecious species, and, furthermore, these flowers are not very closely aggregated in inflorescences. But in andromonoecious Umbelliferae the flowers are small, clustered together, and even occur in dense capitate heads (Webb, 1980). However, the temporal separation of male and female phases in bisexual flowers, as well as at the level of inflorescences and individuals, is very pronounced (Müller, 1883; Cruden & Hermann-Parker, 1977).

Second, male sterility in hermaphroditic flowers may evolve when the optimal conditions for female reproductive success (pollen receipt) and for male repro-

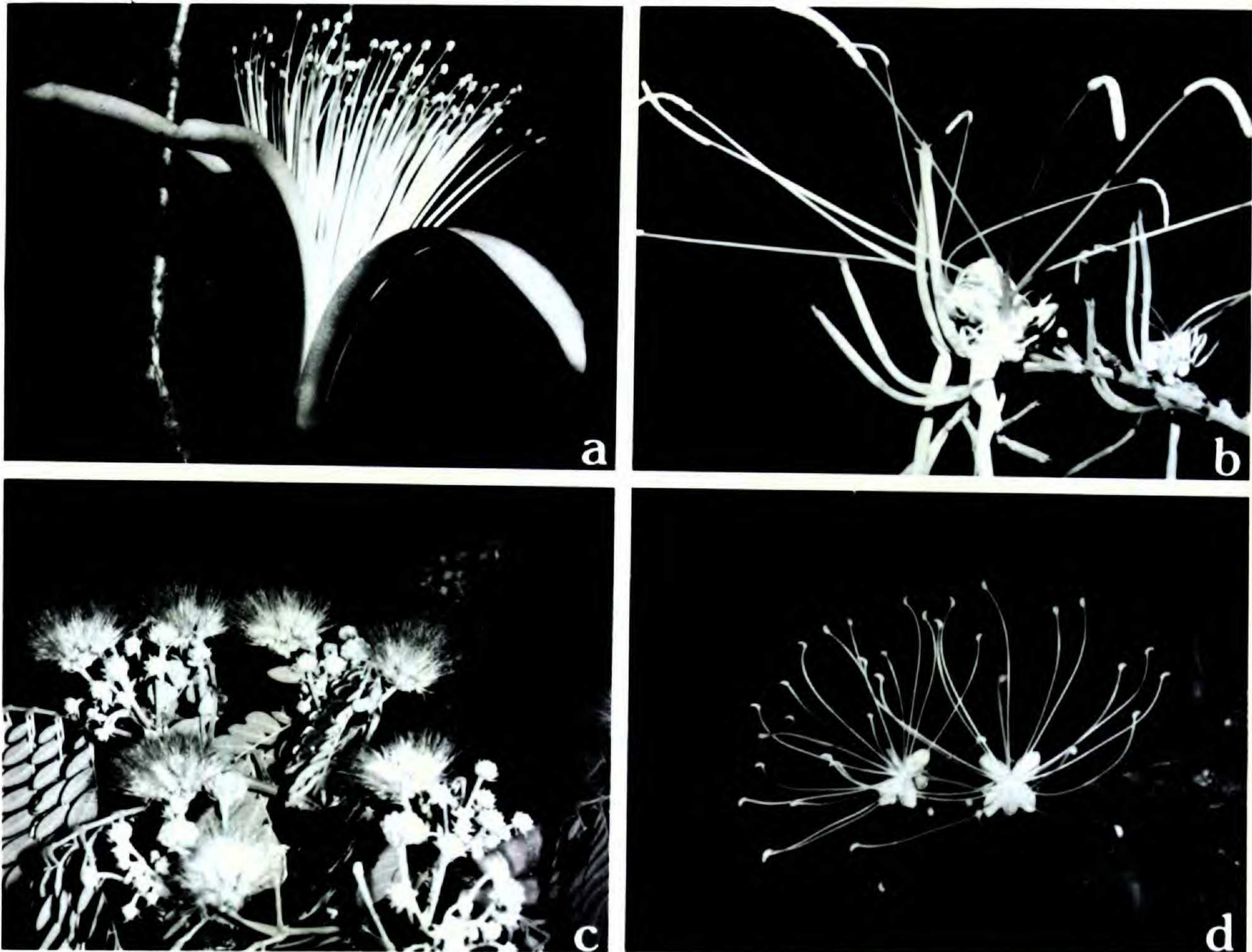


FIGURE 1. Hermaphroditic flowers of *Bombacopsis quinata* (a), *Bauhinia pauletia* (b), *Pithecellobium saman* (c), and *Capparis* sp. (d), to show the importance of stamens in the maintenance of andromonoecism (see text for details). All species, except the particular species of *Pithecellobium* shown here, are andromonoecious; however, andromonoecism has been found by us in some species of *Pithecellobium* closely similar to this particular species. The species are from lowland dry deciduous forest in Costa Rica; Photographs (a) and (b) are by P. A. Opler.

ductive success (pollen donation) are vastly different and strongly influenced by the position of male and female flowers (Heslop-Harrison, 1972). For example, in zoophilous plants where pollinators typically forage from the bottom towards the top in one-day inflorescences, one may expect female flowers at the bottom and male at the top of the inflorescence, as is the case in many monoecious species of the Euphorbiaceae.

Under certain conditions pollinators may select against the loss of sterilization of stamens in the hermaphroditic flowers of andromonoecious species; they thereby impose constraints upon the evolution of andromonoecism towards monoecism. For example, in those cases where the stamens play a large role in the integrity of the pollination system, there would be strong selection against their loss. In andromonoecious species such as *Bauhinia pauletia*, *Bombacopsis quinata*, and *Capparis pitteri* the loss of stamens would destroy the integrity of the flowers or the attractiveness of the inflorescence (Fig. 1). In many mimosoid legumes, the organization of the flowers is largely dependent upon stamens (Fig. 1c) so that one would not expect the andromonoecious species (known to occur in *Albizzia*, *Calliandra*, and *Pithecellobium*, W. Haber, pers. comm.) to evolve

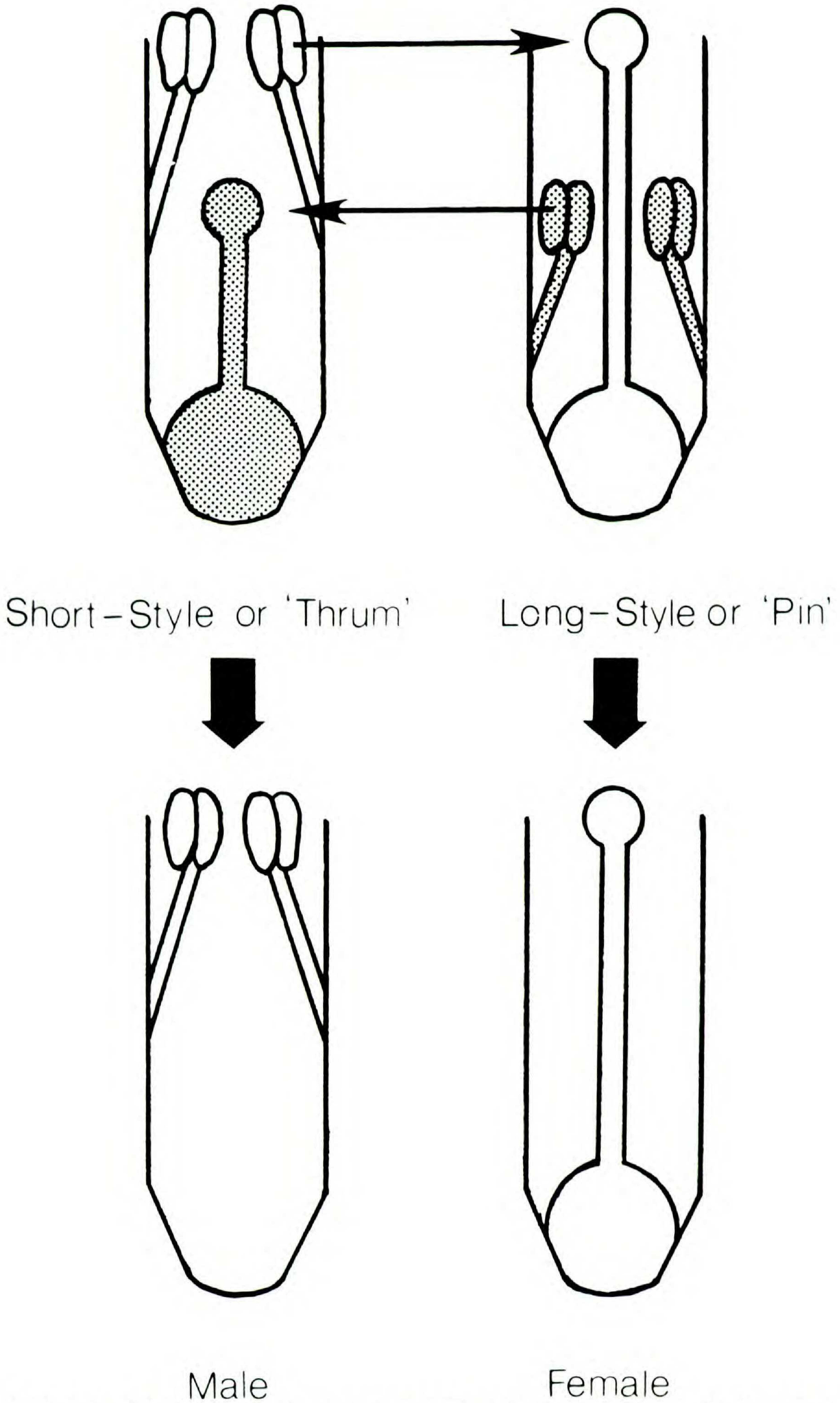


FIGURE 2. Flower forms of distylous species and derived dioecious taxa. The thin arrows between the upper pair of flowers indicate the pollinations that result in fertilization in distylous plants.

into monoecious taxa. In *Solanum*, another genus where andromonoecism is common, stamens may not only play a part in the attraction of the pollinators, but also offer the sole reward to the pollinators since the flowers contain no nectar (Anderson, 1980; W. Haber, pers. comm.). In andromonoecious *Leptospermum* of the Myrtaceae stamens again may be crucial in attracting the flower visitors (Primack & Lloyd, 1980). For *Aesculus pavia*, Bertin (1981) suggested the role of pollen as a food reward in preventing the evolution of andromonoecism to monoecism.

It is not certain if monoecism generally evolves from andromonoecism. There is little discussion of different evolutionary pathways to monoecism in the literature (but see Lloyd, 1972a, 1972b, 1975b). Regardless of the evolutionary pathways involved, selective forces other than those associated with pollination may have also played a role in the evolution of this sexual system.

Heterostyly.—The flower heteromorphisms characteristic of distyly and tristyly have from the earliest study been recognized as structural adaptations to promote disassortative pollination, i.e., the movement of pollen between incompatibility groups (Darwin, 1877). Heterostyly was probably the first sexual system to be recognized as partly an ecological phenomenon.

Distyly, the most common expression of heterostyly is usually associated with gamopetalous, tubular flowers and pollination by relatively long-tongued lepidopterans, hymenopterans, or hummingbirds. The significance of this tripartite relationship among the sexual system, flower morphology, and mode of pollination lies in the fact that the efficacy of pollen transfer from short stamens to short styles (or long stamens to long styles) is contingent upon the deposition of pollen at different locations on the mouth parts of the pollinators. The corolla tube must be relatively long and narrow to allow only restricted access by nectar-seeking probes in order to assure the accurate localization of pollen deposition on the vector, thus promoting subsequent pollen transfer between stamens and styles of the same length.

Most heterostylous species are self-incompatible (Ganders, 1979). The evolution of the self-incompatibility system, which prevents both self-fertilization and mating between plants of the same flower form, probably occurred before the rise of the associated floral heteromorphisms (Ganders, 1979). It is most likely that the morphological features of distyly and tristyly, as part of the pollination system, arose as a response to the appearance of a limited number of incompatibility groups in order to increase disassortative (compatible) pollination and thus a plant's reproductive output (Ganders, 1979; Beach & Kress, 1980). Clearly, both the function and the adaptive basis for the evolution of heterostyly can only be understood by considering the breeding system as an ecological phenomenon: an adaptation to manipulate pollinator movements and pollen flow.

The role of pollinators in the evolution of sexual systems is demonstrated more markedly by the conversion of distyly into dioecism (Fig. 2). This change,

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The heavy vertical arrows represent the evolutionary pathways that have given rise to unisexual flowers. Vestigial styles and stamens are not shown in unisexual flowers. In most cases the change from distyly to dioecy is accompanied by a reduction in the size of the corolla tube. (See Beach & Bawa, 1980, for details)

from one outbreeding system to another has occurred in several genera in the families Boraginaceae and Rubiaceae (Baker, 1958; Lloyd, 1979b; Beach & Bawa, 1980). In every known case where dioecism has evolved in this way, the ancestral long-style form has become female, and the short-style plants have become males (Fig. 2). This would not be the result if selection for unisexuality was unrelated to the ancestral flower condition. Beach & Bawa (1980) have proposed that such a switch from distyly to dioecism is most likely the result of a form of pollinator-mediated selection for femaleness in the long-style and maleness in the short-style form. In *Coussarea talamancana* Standley (Rubiaceae), the evolution of dioecism is probably the result of a switch in the pollinating fauna from moths that are the characteristic pollinators of the genus *Coussarea* in Costa Rica, to short-tongued bees that are incapable of reaching the lower floral organs (short-styles and short-stamens). Lloyd (1979b) and Beach & Bawa (1980) discuss additional genetic and ecological features of the evolution of dioecism from distyly.

Protandry and Protogyny.—The terms *protandry* and *protogyny* have been used at the level of the individual, for example, to describe changes in sex expression between reproductive seasons in perennial monoecious plants (Frankel & Galun, 1977). In contrast, the terms are conventionally reserved by zoologists to describe changes in sex expression that occur only once during the life of an organism (Heath, 1977). Protandry and protogyny are used here with reference to plants that display dichogamy within a single reproductive season and, more specifically, that usually undergo a male-female or female-male transition within a period of a few days, or as little as a few hours. The terms are also applied here with reference to the relative timing of male and female functions within a flower or at most an inflorescence.

Dichogamy is generally assumed to be an adaptation to limit self-pollination and to promote cross-pollination (Müller, 1883; Proctor & Yeo, 1972; but see Onyekwelu & Harper, 1979; Lovett-Doust, 1980). Undoubtedly, differences in the timing of anther dehiscence and stigma receptivity influence the amount of incoming and outgoing pollen. However, if selective pressure for outcrossing was the only factor involved in the evolution of protandry and protogyny, one would expect these systems to occur in almost equal frequencies and to be distributed randomly throughout the flowering plants. But protandry is far more common than protogyny (Burtt, 1977), and, as discussed below, protogyny seems to be largely confined to certain taxonomic groups and pollination modes.

Protandry should be very common in flowering plants for two reasons. First, intrasexual selection or intraspecific competition for mates should promote the dispersal of a plant's pollen before conspecific stigmas have received pollen from other genotypes (see also Webb, 1981). At the same time, selection should favor the receptivity of the stigma when the pollinators have removed pollen from a diverse array of genotypes. On these considerations alone, one may expect protandry to be an almost universal feature of flowering plants, but since this is not the case, the factors that result in the evolution of protogyny will be explored below.

Second, the fact that pollen but not the ovules undergo dispersal makes the conditions for the evolution of protogyny more stringent than those for protandry. Consider, for example, a population consisting of outcrossing individuals in which the hermaphroditic flowers that open on a given day last only for that day (e.g.,

sunrise to sunset). In such a population protogyny can not evolve unless one presumes the pollinators are carrying substantial amounts of pollen from the foraging undertaken in the previous day. However, in the same population all plants can be simultaneously protandrous because the stigmas can be matured later after some pollen has been deposited on the bodies of the pollinators. As the longevity of the flowers increases, the conditions for the evolution of protogyny become less stringent. Thus in hermaphroditic species, protogyny might only evolve when the processes of pollen receipt and pollen donation in a flower are extended over one daylight period. As discussed below, the flowers of many protogynous species indeed do extend beyond one day. Although extensive data on flower longevity for hermaphroditic angiosperms as a whole are lacking, flowers last one day (i.e., one daylight period) in the vast majority of hermaphroditic plants in the tropics. In many of these species almost all pollen is removed within a few hours after anthesis in early morning, but the peak in nectar production is attained in late morning or early afternoon (Frankie et al., 1981; G. W. Frankie & W. Haber, pers. comm.). Presumably pollen in these species is deposited on the stigmas as pollinators continue to forage for several hours after the pollen has been removed. The late deposition of pollen is also indicated by slight exertion of stigmas in some of these species in late morning. Although direct evidence for protandry is lacking in these species, they certainly are not, and cannot be, protogynous under the given conditions of flower longevity and the pollinator foraging behavior.

The differences between male and female gametes in dispersal imposes an additional requirement to the evolution of protogyny. Because of the reasons outlined above, unlike protandry, the operation of protogyny is dependent upon some plants being in the male and others in the female phase at a given time. This is usually brought about by asynchronous development of flowers and inflorescences, as for example in the species of the Annonaceae, Araceae (Fig. 3), Cyclanthaceae, Moraceae, and Palmae. In other species, for example in *Persea gratissima*, plants are dimorphic with respect to the timing of male and female phases: in one type the flowers in the female stage open in the morning and then close in the afternoon to reopen in the male stage the following afternoon; in the other type the flowers open in the afternoon in the female stage and then in the male stage in the following morning (Stout, 1924).

The evolution of protogyny can be traced to three aspects of pollination biology. First, protogyny has coevolved in conjunction with several specific life-history aspects of pollinators. In many species of Magnoliaceae, Annonaceae, Araceae, Cyclanthaceae, and Palmae (among others), protogyny is associated with cantharophily (Faegri & van der Pijl, 1971; Bawa & Beach, unpublished observations). The pollinating beetles fly in the late afternoon or early evening to flowers (or inflorescences) while carrying pollen from other conspecific plants and then crawl into some type of enclosure formed by spathes, bracts, or perianth parts and while doing so, deposit pollen on stigmatic regions; after spending the night and most of the following diurnal period in the enclosures, the beetles emerge to fly to another flower or inflorescence usually on a different individual (Fig. 3). Pollen is released just prior to the beetles' departure. The important aspect here is not the pollination by beetles per se, but: (1) the time of beetle flight behavior, (2) the long residency of the pollinators in floral structures, and

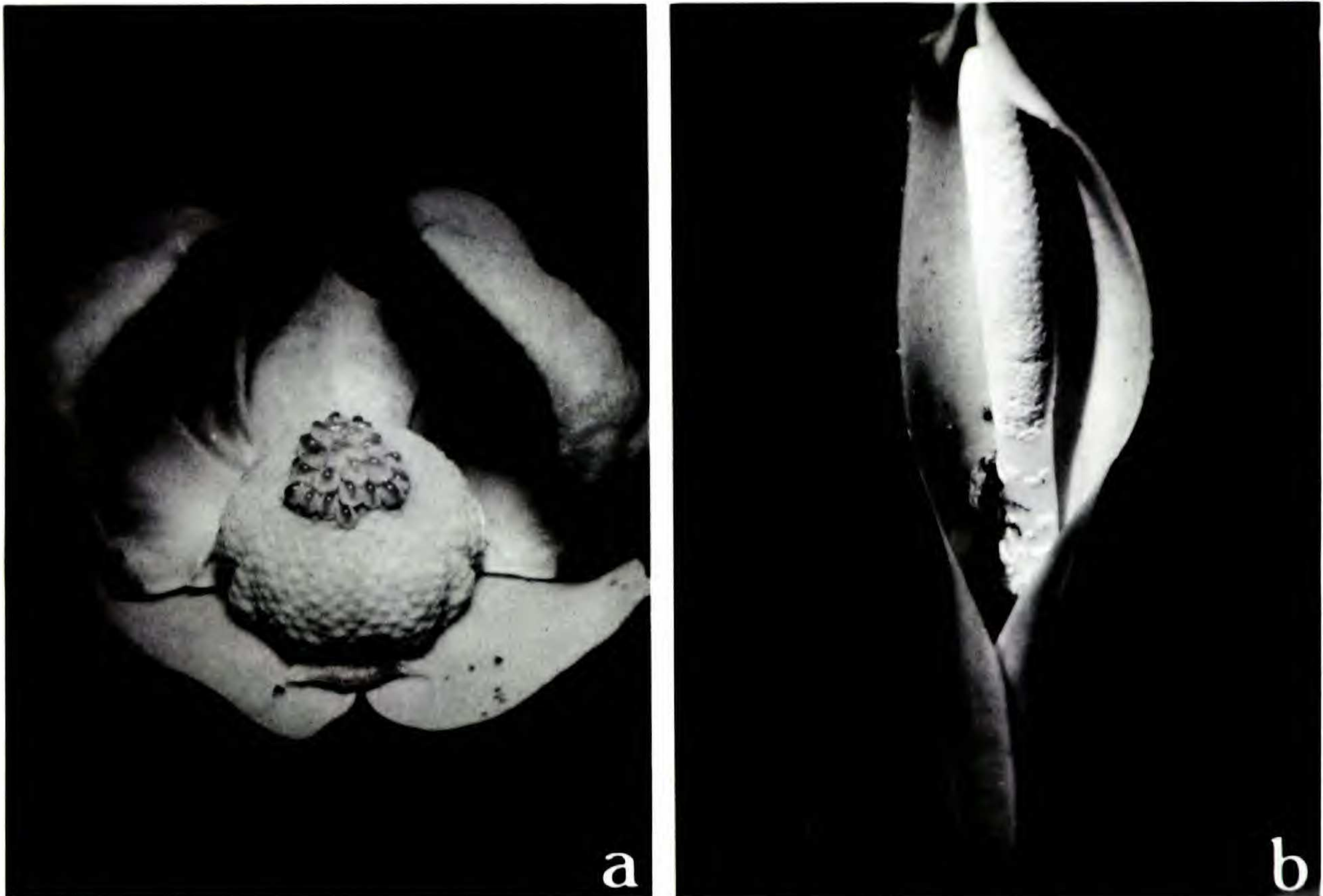


FIGURE 3. Flower of *Cymbopetalum* sp. (a) and an inflorescence of *Dieffenbachia* sp. (b). A petal of the *Cymbopetalum* flower has been removed to show the exudate on the receptive stigmas and the tightly packed stamens surrounding the gynoecium. The inflorescence of *Dieffenbachia* bears female flowers at the bottom, the portion shown to be completely enclosed by the spathe, and male flowers at the top, the portion shown to be exposed. Both the species are from a tropical lowland wet evergreen forest in Costa Rica.

(3) one foraging trip every 24 hours. Recall that in *Ficus*, a genus in which protogyny is an universal feature of the monoecious species, the prolonged inhabitation of wasps is also associated with just one trip between the pollinated and the to-be-pollinated figs (Ramírez, 1969). It is apparent that the type of beetle pollination in the families mentioned above, and pollination by fig wasps could not operate and would not evolve in association with protandry.

Second, selective pressure against the clogging of stigmas by a plant's own pollen may result in the evolution of protogyny. The self-pollen may interfere with the deposition of incoming pollen and/or compete with it for germination sites (Bawa & Opler, 1975). The possibility of clogging increases when the flowers are closely aggregated (Burt, 1977) and the pollination mechanism is imprecise. There are no observations or data that relate the amount of self-pollen received by the stigma (after the termination of the female phase in protogynous species) to the precision of pollination in either the protogynous or the nonprotogynous taxa. This explanation is different from the traditional explanation that seeks the evolution of protogyny in selective pressures favoring outcrossing, because it removes the difficulty of explaining the occurrence of protogyny in self-incompatible species (see for example Burt, 1977). Clogging in self-incompatible as well as self-compatible species decreases the amount of incoming pollen that can be deposited on the stigma, as well as the amount of outgoing pollen. Lloyd &

Yates (1981) have used a similar explanation to account for the evolution of protandry in *Wahlenbergia albomarginata*.

Third, uncertainty of cross-pollination may also select for protogyny. Pollen from the anthers of the same flower could be used for pollination if the initial effort in securing cross-pollination were to fail. Protandry may offer no such possibility. It is notable that protogyny is quite common among herbaceous plants that flower early in spring in the north temperate zone, when the conditions for cross-pollination are unpredictable (Schemske et al., 1978).

The consideration of the evolution of protandry and protogyny is complicated by the fact that the plants can be protandrous at the level of the individual and protogynous at the level of flowers and inflorescences or vice versa. For example, most species in the Umbelliferae are protandrous, and the species in which protogyny has been reported have the first order umbels consisting only or mostly of male flowers (Bell & Lindsey, 1978). Thus the so-called protogynous species are, in most cases, actually protandrous. From the evolutionary viewpoint it is the individual-level phenomena that are of interest. However, our phenological knowledge of differential maturation of male and female parts is in most cases restricted to flowers or inflorescences.

SEXUALLY DIMORPHIC SYSTEMS

Dioecism.—Dioecism is widespread in flowering plants. Many attempts have been made to explain its evolutionary basis, and until recently, most evolutionary models have dealt with the genetic benefits of outcrossing as the selective force of most importance (Charlesworth & Charlesworth, 1978; Maynard Smith, 1978; and references therein). Although there is some empirical evidence to support the outcrossing argument (Lloyd, 1981), several alternative models to explain the evolution of dioecism have been proposed (Charnov et al., 1976; Charnov, 1979; Willson, 1979; Bawa, 1980a; Givnish, 1980; Beach, 1981). We will not review all of these recently published proposals, but rather briefly examine those models that deal with the consequences of pollinator foraging behavior on the evolution of the sexual systems.

Most dioecious plants are insect pollinated (Bawa, 1980a), although in the north temperate zone there seems to be an association between dioecism and wind pollination (Freeman et al., 1980). Among the zoophilous taxa, an unusually large number of species are pollinated by small bees or flies (Bawa & Opler, 1975). This correlation between dioecism and pollination by small insects occurs at the taxonomic as well as at the community level of organization (Bawa, 1980a). Three attempts have been made to elucidate the ecological and evolutionary basis of this correlation.

According to Givnish (1980) pollination by small opportunistic insects is inefficient in the sense that they mediate little interplant movement of pollen. Thus, increases in male reproductive effort (in originally hermaphroditic plants) do not result in corresponding increases in paternal fitness. In contrast, Givnish argues that an increase in maternal reproductive investment (e.g., the maturation of more fruits) should result in a disproportionate gain in female fitness. As a consequence, he proposes that female individuals could successfully invade an hermaphroditic

population, and then create conditions favorable for the evolution and establishment of males.

Bawa (1980a) and Beach (1981) have argued that pollinators such as small generalist bees respond dramatically to changes in floral displays. Thus an increase in flower number on an hermaphrodite may lead to a disproportionate increase in male fitness because plants with larger floral displays may either attract more pollinators and thereby disperse more pollen, or be visited earlier in the day and thereby transmit more genes via pollen than via ovules. The variation in flower number may result from intrasexual competition or may be a part of the normal variation in a natural outcrossing population. As a consequence of this variation and the type of pollinator-mediated selection described here, males would be established. Females may become established when individuals with a smaller number of flowers increase their fitness due to resources saved from reduced pollen dispersal costs (see Bawa, 1980a, for other factors leading to the establishment of females).

Lloyd (1981) has suggested that dioecism is more likely to arise in species serviced by small promiscuous insects because pollination by such pollinators would result in a high level of selfing in self-compatible species.

Regardless of which factor has contributed more to the observed correlation, the involvement of pollinators in the evolution of dioecism cannot be denied.

Gynodioecism.—The evolution of gynodioecism involves the establishment of male-sterile mutants in a population consisting of hermaphrodites. There is evidence that selective pressure for outcrossing is responsible for the spread of such mutants (Lloyd, 1981, and references therein). Thus, at this time, pollinator-mediated selection cannot be invoked to explain the evolution of gynodioecism, though it is noteworthy that the majority of gynodioecious species are also pollinated by small insects (D. G. Lloyd, pers. comm.).

Gynodioecism usually evolves into dioecism by the gradual loss of female fertility of the hermaphrodites (Lloyd, 1975a; Charlesworth & Charlesworth, 1978). Selective pressures underlying the conversion of hermaphrodites into males are not fully understood; however, according to Charlesworth & Charlesworth (1978), an increase in pollen production is a requirement. If production were equated with dispersal, increased dispersal could result from pollinator-mediated intrasexual competition for the females, especially if the gain in fitness from increased dispersal outweighed the loss of fitness due to the elimination of female functions. It is noteworthy that in the Umbelliferae, dioecious species have a higher male/female flower ratio than the gynodioecious species (Webb & Lloyd, 1980). It is possible that an increase in male flower number in dioecious species has resulted from intrasexual competition.

Androdioecism.—The establishment of males in a population consisting of hermaphrodites results in the evolution of androdioecism. It is generally assumed that selective pressure for outcrossing does not result in the evolution of androdioecism because in a selfing population, the ovules of hermaphrodites are not readily available to male plants (Lloyd, 1975a; Charlesworth & Charlesworth, 1978). In the absence of selfing, the pollen production of males must be more than twice that of hermaphrodites in order for androdioecism to evolve. Such a dramatic increase in pollen production (and dispersal) may be possible when

pollination is effected by pollen collecting visitors (see also Ross, 1980). Androdioecism has been reported in some species of *Solanum* (Symon, 1979). The flowers of *Solanum* produce no nectar; pollen is the only reward to pollinators, which are pollen-collecting bees. We would predict that most additional examples of the evolution of dioecism from andromonoecism are likely to be reported from bee-pollinated species.

DISCUSSION

We have shown that the influence of pollinators in the evolution of sexual systems stems from a multitude of interactions between plants and pollinators: (1) ability of pollinators to respond to minor changes in floral resources, thereby altering the patterns of pollen donation and pollen receipt (evolution of dioecism); (2) need in plants to retain structures crucial to the integrity of the pollination system (maintenance of andromonoecism, androdioecism); (3) a single foraging trip by the pollinators to flowers or inflorescences associated with long inhabitation in these structures to find mates, avoid predators, or gather food (evolution of protogyny); (4) interference between pollen removal and pollen receipt in plants with small flowers pollinated by unspecialized insects (evolution of monoecism); and (5) precise deposition of pollen on the long mouth parts of pollinators to promote compatible pollinations (evolution of heterostyly). Although we have cited examples where other factors may have been more important, we do not deny the role of outcrossing in the evolution of sexual systems. Different selective forces may operate at different levels. Selection for outbreeding or for an optimal amount of recombination may explain why plants are cross- or self-fertilized, while sexual selection, including pollinator-mediated selection, may explain why outcrossing is achieved in different ways, or why some species are hermaphroditic, others andromonoecious, monoecious, gynomonoecious, dioecious, gynodioecious, or androdioecious.

We have so far considered only spatial and temporal patterns of floral sexuality. It is, however, worth emphasizing that the evolution of self-compatibility and self-incompatibility too is not independent of pollination events. In several taxa, the evolution of self-compatibility has been traced to the paucity of pollinators due to inclement weather (Hagerup, 1951), competition for pollinators (Levin, 1972), changes in pollinator fauna (W. B. Haber & G. W. Frankie, pers. comm.), and the traplining behavior of pollinators that precludes the necessity for physiological self-incompatibility (W. J. Kress, pers. comm.). Self-incompatibility or the ability to discriminate between self- and cross-pollen has evolved only in angiosperms. The flowering plants are also unique in the sense that only in this group does a large number of diverse pollen genotypes land on the stigma as a result of animal pollination (Mulcahy, 1979). In gymnosperms, for example, very few pollen grains reach the pollination chamber (Stern & Roche, 1974). Fisher (1958: 143) was the first to consider the theoretical significance of discrimination against different pollen genotypes in the context of sexual selection. He cited the work of Jones (1928) on G_3 factors in maize to underscore the fact that the discrimination can also involve pollen from different genotypes within the same species, and is not necessarily restricted to self- versus cross-pollen.

We have argued that the evolution of sexual systems is constrained by the

way the pollinators interact with flowers. But, except in a few instances, we have been unable to predict the type of sexual system that would coevolve with a particular feature of pollination. The tremendous diversity of plant sexual systems and their secondary modifications, the wide variety of pollinators and their diverse behaviors, and the lack of general knowledge about the ecological relationships between sexual systems and pollinators make it difficult to develop a general hypothesis. In addition, we have considered sexual systems within the existing classification, but the classification is based on the morphological description of sexual systems, and is inadequate for several reasons.

First, the purely morphological description masks a considerable amount of quantitative variation within different systems. A number of recent studies (Bawa, 1974; Zapata & Arroyo, 1978; Willson & Price, 1977; Schemske, 1980) have quantitatively demonstrated what has been widely observed in hermaphroditic flowering plants: in many species only a small minority of flowers function to produce seeds and fruits. When traditional sexual system criteria are used to evaluate morphological or intrinsic gender estimates, all these species are classified as hermaphroditic on the basis of potential flower function or preanthesis gender. However, if the actual performance of the flowers is taken into account with estimates of functional gender or effective gender, we must conclude that since most flowers function at most as pollen donors, the sexual system of most hermaphroditic species would be more accurately described as andromonoecious. Thus, when gender estimates which include postfertilization events, or at least the probability of male and female function, are contrasted to prefertilization estimates, we note that the same species could be characterized to have two different systems under the existing classification.

A second inadequacy of our current classification is that it falls short of fully describing the temporal distribution of sexual function in a species. The consideration of the temporal dimension changes the properties of the sexual system deduced from morphological grounds alone. A monoecious plant that matures male flowers first and female flowers several days after the male phase does not have the same sexual system as a plant in which male and female flowers mature more or less at the same time. Furthermore, the plant is neither protandrous in the same way as a plant with hermaphrodite flowers, nor is it dioecious, as such plants are sometimes described in the absence of information concerning the temporal sequence of male and female flowers (Bawa, 1977).

Finally, the morphological classification does not take into account the way the system functions. Faegri & van der Pijl (1971), in discussing such well-known examples as the heads of Compositae, Dipsacaceae, and some Leguminosae, point out that in many cases the morphological differences between flowers and inflorescences are in themselves irrelevant in pollination ecology. More important, in the context of this discussion, these differences can also be irrelevant in the characterization of sexual systems. Consider, for example, the two scarab beetle-pollinated genera, the hermaphroditic *Cymbopetalum* (Annonaceae) and, the monoecious *Dieffenbachia* (Araceae) (Fig. 3). The beetles visit these species in the manner described above under *Protandry and Protogyny*. In brief, incoming beetles bearing pollen from other individuals inhabit the protogynous flowers (*Cymbopetalum*) or inflorescences (*Dieffenbachia*) for about 24 hours and then

after the flower or inflorescence completes the male phase, leave in search of additional plants carrying pollen from the flowers or inflorescences just inhabited. The pistils in the *Cymbopetalum* flowers receive pollen in the same way as the female flowers of the *Dieffenbachia* inflorescence, and similarly the stamens release pollen in the same way as the male flowers of the aroid. Thus, from a functional view the *Cymbopetalum* flower is an analogue of *Dieffenbachia* inflorescence. Current sexual system classification obscures the role of the monoecious inflorescence as a functional unit. In such a situation, then, it does not seem particularly useful to debate the selective forces responsible for the retention of primary hermaphroditism or the evolution of monoecism unless the dynamics of the pollination biology are taken into consideration.

We conclude with the following:

1. The sexual systems of species are fundamentally linked to the pollination biology of the plants and in many instances can only be understood within the context of the pollination system. We suggest, therefore, that further theoretical considerations as to the adaptive nature of sexual systems must consider in more detail the reproductive ecology of the plants.

2. The taxonomy of sexual systems is largely determined by the type of gender estimates taken at the level of the individual. Intrinsic gender estimates and those based on morphological appearance are not as valuable as estimates of functional or effective gender for determining how floral sexuality actually functions and similarly for illuminating variation in effective gender between conspecific plants. The documentation of this variation is of great utility for understanding the selective forces and evolutionary pathways of sexual system evolution.

3. The temporal dimension of plant sexuality is greatly underestimated by current classification schemes which are largely based on spatial features of plant gender.

4. The morphological distinction between flowers, inflorescences, and even larger groups of flowers such as the totality of flowers in a tree canopy is maintained for most general purposes, but it must also be realized that these units of attraction and/or function might be irrelevant as far as the pollinators are concerned. Consequently, our sexual-system classification is to an extent arbitrary, as class limits are defined on the basis of morphological features and not on the basis of actual function.

5. Finally, we conclude that viewing plant sexual systems with vague reference to the regulation of genetic recombination is unlikely to account fully for the evolution of sexual systems and that the key to understanding them lies in considering patterns of sexuality as means of optimizing male and female reproductive success in different ways within the constraints imposed by the pollination system.

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